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Succession and activity of microarthropods and enchytraeids during barley straw decomposition

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With 2 figures

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1. Introduction

Soil animal participation in plant litter decomposition has been investigated in several field experiments. In most cases litter-bag techniques have been used. The majority of studies have been devoted to forest ecosystems (ANDERSON 1975; MIGNOLET & LEBRUN 1975; BERG *et al.* 1980; HÅGVAR & KJÖNDAHL 1981), arid ecosystems (SANTOS & WHITFORD 1981; ELKINS & WHITFORD 1982), peat bogs (STANDEN 1978) or grasslands (BOCOCK 1964; CURRY 1969; VOSSBRINCK *et al.* 1979; DICKINSON 1983). There are only a few studies in arable systems (NAGLITSCH 1966; EITMINAVIČIŪTĖ *et al.* 1976; ANDRÉN & LAGERLÖF 1983; CZARNECKI 1983).

Several biological and chemical aspects of barley straw decomposition, i.e., mass loss, chemical changes and microbial biomass, were investigated in a two-year litter-bag experiment in arable soil. Results from decomposition and fungal investigations are reported by WESSÉN & BERG (1985), nematode abundance and activity by SOHLENIUS & BOSTRÖM (1984) and a synthesis of the experiment is underway (O. ANDRÉN *et al.* unpubl.). The present paper concerns the microarthropods and enchytraeids in this experiment.

The aim of the study was to assess arthropod and enchytraeid contribution to substrate decomposition, as indicated by their respiration and consumption. We also tested whether a microarthropod succession of species could be correlated to changes in substrate quality and activity of other soil organisms, and if the fauna of decomposing straw was different from the overall soil fauna.

2. Material and Methods

The study area is located at Kjettslinge, Örbyhus estate (60° 10′ N, 17° 38′ E) about 40 km north of Uppsala in south central Sweden, 30 m above sea level. The climate is cold temperate with a long-term, mean annual temperature of +5.4 °C. The mean temperature for the coldest month is —5.4 °C (February) and for the warmest, +16.7 °C (July). The long-term, mean annual precipitation is 520 mm with maximum in late summer and minimum in late winter. The topsoil is a loam with 20% clay, 1.6 to 3.1% carbon and a *p*H in water ranging from 6.0 to 6.5. For a comprehensive site description see STEEN *et al.* (1984).

The barley straw was collected at normal harvest time from a field fertilized with 80 kg N ha^{-1} $year^{-1}$. Leaves were removed and the straw was cut into 2 to 4 cm pieces and dried at room temperature to constant mass. The nitrogen content was 0.6% of organic matter. More information on chemical composition will be found in WESSÉN & BERG (1985). The straw was put in 15×15 cm terylene net bags with 1 mm mesh size, 2.50 g in each.

Spring barley (*Hordeum distichum* L. cv. GUNILLA), receiving no nitrogen fertilizer, was grown in the plot during the experiment. In the preceding growing season barley was also grown, receiving 90 kg P and 168 kg K ha^{-1} and no nitrogen fertilizer. Harvest was in early September 1980 and the straw was removed. The roots and stubble (200 g m^{-2}, A.-C. HANSSON pers. comm.) were ploughed into the soil on 23 October. One thousand litter-bags were incubated in the field at depths of 10 to

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15 cm on 4 November 1980. The plot was resown in May 1981, harvested in September and the straw was removed. The plot was left unploughed during winter 1981/1982 and was rotatilled to a depth of 5 cm before sowing in May 1982. This gave an input to the soil of roots and stubble similar to that in autumn 1980. The harvest and straw removal was done as in 1981. The soil was left unploughed until the end of the experiment on 20 October 1982. The experiment lasted for 720 days.

Litter-bags were collected on 11 occasions for microarthropod and enchytraeid extraction from individual bags, 20 bags (10 in the last sampling) and 5 bags, respectively. Microarthropods were extracted by the high-gradient canister method (MACFADYEN 1961; PETERSEN 1978; ANDRÉN 1985) for five days under a temperature increase from 20 to 45 °C. Enchytraeidae were extracted by the wet funnel technique described by O'CONNOR (1962).

In the microarthropod samples, Collembola and Acari were determined to species or genera. If determination to these levels was not possible higher levels were used (e.g., Eupodidae were divided into three size classes). Other arthropods were combined into larger taxonomic groups. In the first four samplings all arthropod specimens in all samples were measured to the nearest 0.05 mm for determination of mean individual and population biomass. In the later samplings animals were measured in five of the 20 litter-bags and, in the last sampling, in three of ten.

Length/mass and, for Acari, length/width/mass regressions were used for individual biomass determinations as described in PERSSON & LOHM (1977). For the most common species an individual biomass was calculated for each sampling occasion, but the rest of the material was too small for determination at each sampling. Therefore, an average biomass for the whole period of exposure was used for these groups.

Enchytraeidae were counted live, and each specimen was measured under a stereomicroscope (10× magnification) and sorted into three size classes, < 2 mm, 2 to 6 mm and > 6 mm. Each size class was given a mean fresh body mass according to relationships described in PERSSON & LOHM (1977). In October 1982 no sampling was done for Enchytraeidae and abundance and biomass were assumed to be equal to those in the September 1982 sampling, which were used in the respiration calculations.

Mean density and standard error (S.E.) were calculated as individuals per litter-bag. Species diversity was calculated for the arthropod community. Both the Shannon-Wiener H′ (SHANNON & WEAVER 1949) and E, the evenness of allotment of individuals among the species (LLOYD & GHELARDI 1964), were calculated.

The microarthropod fauna of the straw litter-bags was compared with the soil fauna at two occasions, September 1981 and 1982. Since the abundance was generally higher in the bags than in the soil, the relative abundance of each taxon was calculated, i.e., the percentage of the total number of microarthropods in the straw and soil, respectively. Comparisons between straw and soil were then made using the relative abundances.

Faunal respiration was calculated from abundance, biomass and temperature (PERSSON & LOHM 1977; PERSSON *et al.* 1980). The relationship used to calculate the respiration of a specimen at a certain temperature (T_0) was $Q = a \cdot W^b$, where Q = oxygen consumption rate (mm^3 ind.$^{-1}$ h^{-1}), W = fresh mass (g), a and b = specific constants for each species or other taxon. The Q values were assumed to be dependent on temperature according to a Q_{10} relationship, depending on the organism and temperature interval under consideration. The RQ conversion factor from O_2 consumption to CO_2 emission was 0.8 (PERSSON *et al.* 1980).

The contributions of different size classes to respiration were not considered. Instead, a mean biomass for each species was used. This results in overestimation of respiration (ÅGREN & AXELSSON 1980), but there are compensatory underestimations included in the methodology, e.g., loss of specimens during sample handling and extraction.

Soil temperature at a depth of 15 cm was measured at 30-minute intervals at two adjacent barley plots in the experimental field, and daily mean (Fig. 1), maximal and minimal temperatures were calculated and used in the respiration calculations. The animal abundances were linearly interpolated between the sampling dates. In the most common species, where different individual biomass means at different sampling dates were calculated, these were linearly interpolated between the sampling dates.

Daily respiration (R_D) (μg C bag^{-1} day^{-1}) for a single species was calculated as:

$$R_D = a \cdot \frac{0.8 \cdot 12}{22.4} \cdot 24 \cdot k \cdot W^b \cdot N$$

where a and b = constants, 0.8 = RQ for CO_2/O_2, 12/22.4 = g C/l CO_2, 24 = hours per day, k = a conversion factor calculated from the daily temperature range, W = species mean fresh mass and N = number of this species per litter-bag.

The k factor was calculated from:

$$k = CF \cdot Q_{10}^{(T_{mean} - T_0)/10}$$

where Q_{10} = constant for the temperature dependence of respiration for a certain taxon, adopted from PERSSON & LOHM (1977), T_{mean} = daily mean temperature, T_0 = the base temperature at which the Q_{10} value was determined, CF = correction factor for diurnal temperature variation.

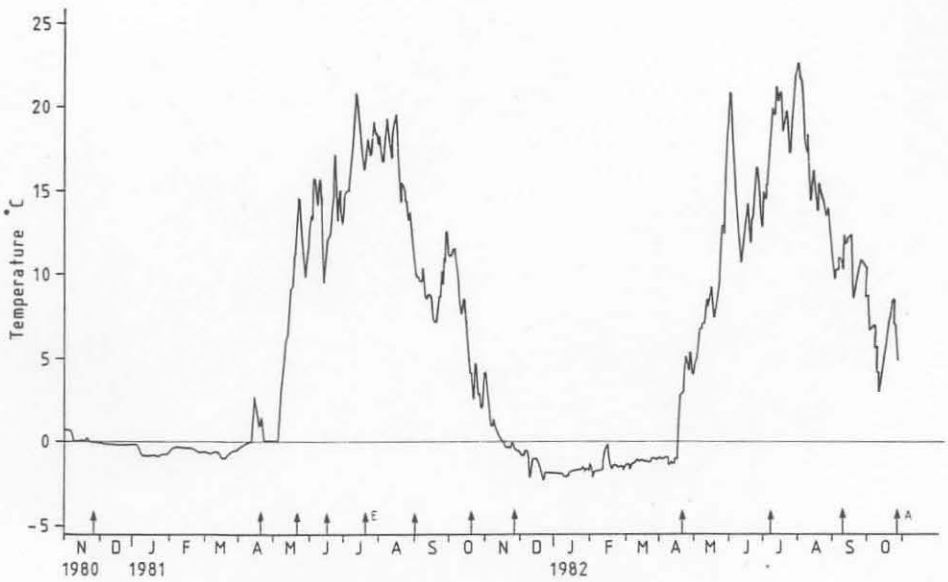

Fig. 1. Daily mean temperature at 15 cm depth, measured at 30 min intervals. Samplings are indicated by arrows (E = only enchytraeids sampled, A = only arthropods sampled).

CF was calculated using the approximation by Ågren & Axelsson (1980):

$$CF = 1 + 0.25 \cdot Z^2 + 0.016 \cdot Z^4 + 0.0004 \cdot Z^6$$

where $Z = \ln Q_{10} \cdot 0.1 \cdot T_{amp}$

$$T_{amp} = T_{max} - T_{min}$$

If diurnal temperature fluctuation is not corrected for, an underestimation of up to 15% may result (T. Persson unpublished).

Production (P), defecation (F) and consumption (C) were calculated for higher taxa from the respiration (R), using the formula $C = P + F + R$ (Petrusewicz & Macfadyen 1970) with energetic quotients adopted from Heal & MacLean (1975).

3. Results

Abundance, biomass and monthly respiration of arthropods and enchytraeids are summarized in Fig. 2. Abundances of specific taxa are given in Table 1.

In November 1980, three weeks after litter burial, the only animals found were Diptera (Chironomidae) larvae (Fig. 2). In April 1981 a few Collembola *(Folsomia fimetaria)* and astigmatid mites *(Schwiebia talpa)* were found (Table 1). In May, 14 arthropod taxa were found in low densities, with *S. talpa* dominating. In June arthropod numbers were still low, but the number of taxa had increased to 27, resulting in the highest diversity (H′) recorded in the investigation (Table 2). Individual biomasses of the most common Collembola were higher in the spring and summer of 1981 than later on in the experiment. For other taxa no such trends could be seen. Enchytraeids appeared in high numbers before the arthropods did, and in June 1981 they reached their highest abundance and biomass.

In July 1981 only enchytraeids were sampled. Their numbers were similar to those in June, but the smaller size classes dominated and only a few individuals > 6 mm were found.

Between June and September 1981 arthropod density increased drastically and reached 92 individuals per bag, representing 28 taxa. From September onwards, the arthropod species composition was similar between the samplings, the four most common species being *S. talpa*, *F. fimetaria*, *Tullbergia krausbaueri* s.l. and *Proisotoma minima*. However, their relative positions shifted from one sampling to another.

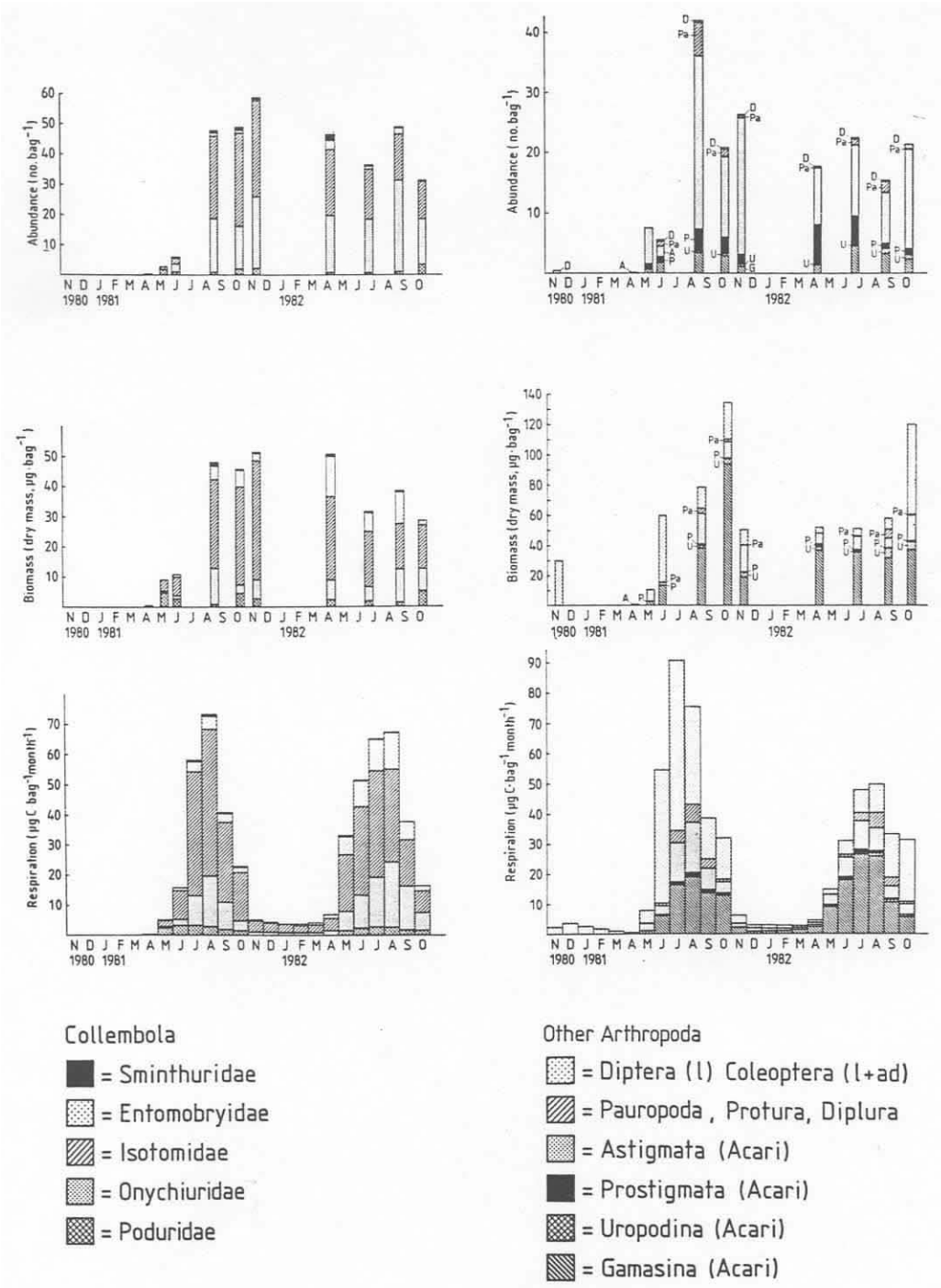

Fig. 2. Abundance, biomass and respiration of Collembola, other arthropods and Enchytraeidae of three size classes. In October 1982 no sampling for Enchytraeidae was made. In the calculations of monthly respiration the abundance and biomass of Enchytraeidae at this date were assumed to be equal to those in September 1982.

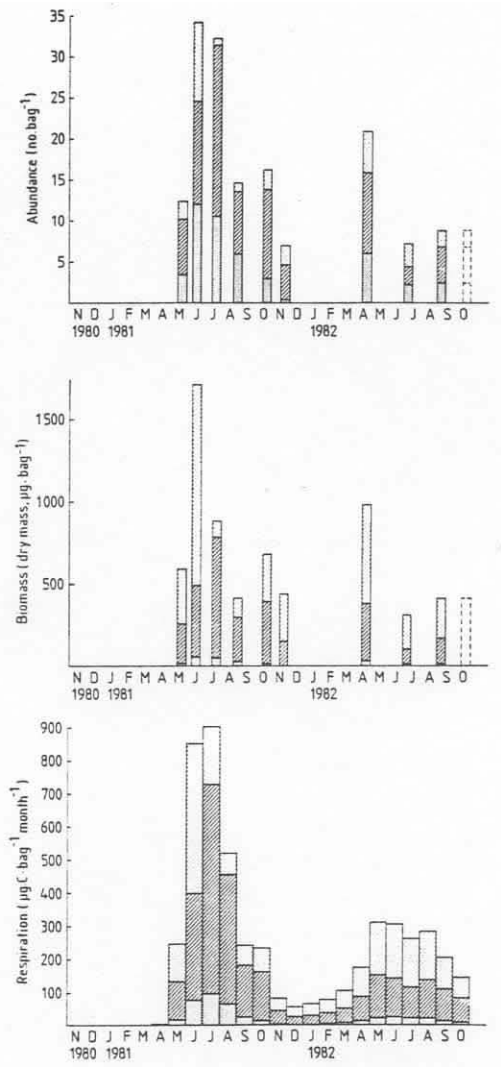
Abundance (no.bag^{-1})
35
30
25
20
15
10
5
N D J F M A M J J A S O N D J F M A M J J A S O
1980 1981 1982
Biomass (dry mass, µg.bag^{-1})
1500
1000
500
N D J F M A M J J A S O N D J F M A M J J A S O
1980 1981 1982
Respiration (µg C.bag^{-1} month^{-1})
900
800
700
600
500
400
300
200
100
N D J F M A M J J A S O N D J F M A M J J A S O
1980 1981 1982
Enchytraeidae, length classes
= > 6 mm
= 2-6 mm
= < 2 mm

Table 1. Individual fresh mass (μg), abundance (No. per litter-bag and standard error), total respiration during the incubation (μg C per litter-bag) for separate taxa and the relative abundance (Percent of total arthropod numbers in the bags or in the soil, respectively) for September 1981/82

Taxon	Ind. fresh mass [μg]	Abundance (S.E.)										Total resp.	Relative abundance			
		1981						1982					1981		1982	
		0420	0519	0616	0901	1020	1124	0420	0706	0907	1026		Soil	Straw	Soil	Straw
Collembola													48.9	54.5	54.7	75.6
Poduridae													0.0	3.5	3.4	2.0
Friesea mirabilis	4.2—9.0	0.0	1.4 (0.5)	0.9 (0.2)	3.2 (0.3)	2.0 (0.4)	2.3 (0.5)	2.7 (0.4)	0.8 (0.2)	1.3 (0.2)	1.8 (0.6)	40.5	0.0	3.5	3.4	2.0
Onychiuridae													30.1	19.3	23.9	46.5
Onychiurus armatus s.l.	3.1	0.0	0.0	0.2 (0.2)	0.2 (0.1)	0.2 (0.1)	0.5 (0.2)	3.0 (0.9)	0.2 (0.2)	0.1 (0.1)	0.2 (0.1)	5.7	0.2	0.2	0.0	0.1
Tullbergia krausbaueri s.l.	0.6—3.0	0.0	0.4 (0.2)	2.4 (0.1)	17.5 (3.8)	14.0 (3.4)	23.1 (3.3)	15.3 (2.3)	17.0 (3.0)	30.1 (4.0)	14.9 (2.0)	117.4	29.9	19.1	23.9	46.4
Isotomidae													18.0	30.0	26.5	23.3
Folsomia fimetaria	3.1—11.9	0.2 (0.1)	0.5 (0.2)	1.4 (0.3)	19.6 (2.4)	19.0 (2.7)	12.2 (1.6)	14.9 (2.2)	12.0 (1.6)	10.4 (1.7)	4.5 (1.0)	231.0	11.5	21.4	25.6	16.0
Isotoma notabilis	6.0	0.0	0.0	0.0	0.0	0.2 (0.2)	0.1 (0.1)	0.4 (0.1)	0.1 (0.1)	0.1 (0.1)	0.3 (0.1)	1.3	0.6	0.0	0.0	0.1
Isotomiella minor	9.4	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	1.7 (0.3)	0.8 (0.3)	1.2 (0.4)	1.6 (1.1)	20.0	5.6	0.0	0.0	1.8
Proisotoma minima	1.5—5.7	0.0	0.1 (0.1)	0.5 (0.3)	7.9 (2.4)	11.6 (2.5)	19.6 (4.3)	4.9 (1.1)	3.7 (0.8)	3.5 (0.9)	6.4 (1.8)	46.9	0.2	8.6	0.9	5.4
Entomobryidae													0.2	1.0	0.9	3.4
Pseudosinella decipiens	23.8	0.0	0.0	0.2 (0.1)	0.3 (0.2)	0.3 (0.2)	0.3 (0.2)	1.2 (0.3)	0.4 (0.2)	0.6 (0.2)	0.0	25.7	0.0	0.3	0.9	0.8
P. alba	13.3	0.0	0.0	0.0 (0.1)	0.6 (0.2)	0.9 (0.2)	0.1 (0.1)	1.2 (0.5)	1.0 (0.3)	1.7 (0.4)	0.3 (0.2)	34.7	0.2	0.7	0.0	2.6
Sminthuridae													0.6	0.7	0.0	0.4
Neelus minimus	0.5	0.0	0.0	0.0	0.7 (0.2)	1.0 (0.3)	0.6 (0.2)	2.0 (0.5)	0.3 (0.2)	0.3 (0.1)	0.2 (0.1)	1.9	0.2	0.7	0.0	0.4
Sminthurinus elegans	17.2	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.4	0.0	0.0	0.0
Misc. Apterygota													4.4	0.0	0.4	0.5
Protura	11.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1 (0.1)	0.0	0.3	4.4	0.0	0.4	0.1
Diplura	52.1	0.0	0.0	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	0.3 (0.3)	0.0	6.0	0.0	0.0	0.0	0.4

Insecta pterygota													3.5	0.2	1.7	1.1
Diptera (larvae)	300.0	0.0	0.0	0.0	0.1 (0.1)	0.1 (0.1)	0.0	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.8 (0.4)	82.9	3.5	0.1	1.7	0.1
Coleoptera (adults)	900.0	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	29.4	0.0	0.0	0.0	0.0
Coleoptera (larvae)	800.0	0.0	0.0	0.2 (0.1)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.0	0.0	0.0	0.0	128.4	0.0	0.1	0.0	0.0
Aphididae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7 (0.5)	0.1 (0.1)		0.0	0.0	0.0	1.0
Acari													26.3	39.1	34.2	20.2
Gamasina													4.8	3.6	8.9	4.9
Alliphis siculus	10.4	0.0	0.4 (0.3)	0.2 (0.1)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.0	0.0	0.0	0.0	2.4	0.0	0.1	0.4	0.0
Hypoaspis aculeifer	18.2	0.0	0.0	0.5 (0.2)	1.2 (0.4)	0.1 (0.1)	0.2 (0.1)	0.4 (0.2)	0.6 (0.2)	0.5 (0.2)	0.0	25.8	0.4	1.2	1.7	0.7
Arctoseius cetratus	6.9	0.0	0.0	0.2 (0.1)	0.6 (0.2)	0.8 (0.2)	0.4 (0.2)	0.2 (0.1)	0.0	0.4 (0.1)	0.2 (0.1)	5.6	1.5	0.7	1.3	0.5
Rhodacarus coronatus	11.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1 (0.1)	0.2 (0.1)	0.0	0.0	1.2	0.4	0.0	0.0	0.0
Rhodacarellus silesiacus	6.4	0.0	0.3 (0.2)	0.6 (0.2)	0.8 (0.2)	0.1 (0.1)	0.0	0.0	3.2 (0.5)	1.2 (0.4)	0.0	22.6	1.0	0.8	5.1	2.0
Dendrolaelaps strenzkei	5.2	0.0	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.0	0.0
Amblygamasus stramenis	148.7	0.0	0.0	0.1 (0.1)	0.4 (0.3)	1.5 (0.3)	0.2 (0.1)	0.6 (0.2)	0.4 (0.1)	0.3 (0.1)	0.4 (0.1)	100.9	1.3	0.4	0.4	0.4
Paragamasus lapponicus	19.5	0.0	0.0	0.1 (0.1)	0.2 (0.1)	0.0	0.0	0.0	0.0	0.1 (0.1)	0.0	3.0	0.2	0.3	0.0	0.1
Veigaia exigua	18.5	0.0	0.0	0.0	0.0	0.2 (0.1)	0.2 (0.1)	0.0	0.2 (0.2)	0.8 (0.3)	1.7 (0.5)	10.8	0.0	0.0	0.0	1.2
Uropodina																
Nenteria breviungulata	19.9	0.0	0.0	0.0	0.2 (0.1)	0.4 (0.2)	0.4 (0.2)	0.2 (0.1)	0.1 (0.1)	0.8 (0.2)	0.6 (0.2)	4.9	0.0	0.2	0.0	1.1
Prostigmata													19.8	3.9	23.6	1.5
Pachygnathidae sp.	0.2	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alicorhagia plumipilus	0.6	0.0	0.1 (0.1)	0.1 (0.1)	0.8 (0.2)	0.4 (0.2)	0.5 (0.2)	0.4 (0.2)	2.0 (0.5)	0.4 (0.2)	0.9 (0.5)	1.9	9.8	0.8	2.6	0.8
Tarsonemus sp.	0.5	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.4 (0.3)	0.0	0.0	0.2	1.0	0.0	2.6	0.0

Table 1 (continued)

Taxon	Ind. fresh mass [μg]	Abundance (S.E.)										Total resp.	Relative abundance			
		1981						1982					1981		1982	
		0420	0519	0616	0901	1020	1124	0420	0706	0907	1026		Soil	Straw	Soil	Straw
Pygmephorus sp.	0.6	0.0	0.1 (0.1)	0.4 (0.4)	1.0 (0.2)	1.8 (0.5)	0.9 (0.3)	1.4 (0.4)	0.1 (0.1)	0.0	0.0	1.3	5.6	1.0	11.9	0.0
Scutacarus sp.	0.5	0.0	0.0	0.1 (0.1)	0.1 (0.1)	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.9	0.0
Eupodidae sp. [< 0.20 mm]	0.2	0.0	0.4 (0.1)	0.3 (0.1)	0.4 (0.4)	0.1 (0.1)	0.2 (0.2)	2.0 (0.6)	1.6 (0.6)	0.2 (0.1)	0.1 (0.1)	0.7	1.5	0.4	0.9	0.3
Eupodidae sp. [0.20—0.35 mm]	0.9	0.0	0.1 (0.1)	0.0	1.4 (0.4)	0.4 (0.1)	0.1 (0.1)	2.0 (0.3)	0.4 (0.3)	0.2 (0.1)	0.0	1.9	1.5	1.5	4.3	0.2
Eupodidae sp. [> 0.35]	2.5	0.0	0.0	0.0	0.1 (0.1)	0.0	0.0	0.4 (0.2)	0.2 (0.1)	0.1 (0.1)	0.0	0.8	0.4	0.1	0.4	0.1
Astigmata													0.4	31.4	1.3	12.8
Anoetidae sp.	1.2	0.0	0.2 (0.1)	0.2 (0.2)	0.0	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0
Anoetidae sp. (hypopus nymphs)	0.5	0.0	0.0	0.2 (0.2)	1.0 (0.4)	0.6 (0.3)	0.1 (0.1)	0.0	0.0	0.0	0.0	0.5	0.0	1.0	0.0	0.0
Schwiebia talpa	1.7—3.2	0.1 (0.1)	6.0 (1.8)	1.4 (0.5)	27.8 (7.4)	12.6 (4.1)	22.6 (5.3)	9.7 (2.3)	12.0 (3.4)	8.4 (2.7)	16.6 (3.9)	83.5	0.2	30.3	0.9	12.8
S. talpa (hypopus nymphs)	0.8	0.0	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Tyrophagus palmarum	1.6	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
Cryptostigmata													1.3	0.0	0.4	0.0
Oppia sp.	0.9	0.0	0.0	0.1 (0.1)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.3	0.0	0.4	0.0
Myriapoda																
Pauropoda	2.3	0.0	0.0	0.7 (0.3)	5.8 (1.3)	1.2 (0.3)	0.4 (0.2)	0.1 (0.1)	1.0 (0.3)	1.7 (0.4)	0.1 (0.1)	21.6	13.8	6.3	7.7	2.5

Note: Taxa only found in the soil were included in the calculations but are not listed in this table. For the most common species, the range of ind. fresh masses calculated for different dates is shown. The abundance calculations are based on 20 litter-bags per sampling date, excepting 1982-10-26 when 10 litter-bags were sampled.

Table 2. Diversity indices for the microarthropod community

Date	No. of species S	No. of indiv. N	Shannon-Wiener H'	Equitability E
81-04-20	2	0.3	0.9	0.92
81-05-19	14	10.2	2.2	0.58
81-06-15	27	11.5	3.8	0.81
81-09-01	28	92.3	3.4	0.69
81-10-20	26	69.8	2.7	0.56
81-11-24	24	85.3	2.8	0.62
82-04-20	24	65.0	3.5	0.77
82-07-06	25	58.8	2.9	0.62
82-09-07	27	65.6	3.0	0.64
82-10-26	19	51.7	2.7	0.66

Note: Species number, total microarthropod abundance per litter-bag, Shannon-Wiener index of diversity and equitability.

Table 3. Respiration (R), Production (P), defecation (F) and consumption (C) for the whole two year incubation period [μg litter-bag^{-1}]

Taxon	Feeding habit	R	P	F	C
Arthropoda, **total**		1,046	638	3,256	4,939
Collembola	Microbivore (100%)	517	344	2,009	2,870
Protura	Microbivore (100%)	0.3	0.3	1.2	1.7
Diplura	Microbivore (100%)	6.0	4.0	23.3	33.3
Diptera larvae	Microbivore (70%)	58.0	38.7	226	322
Diptera larvae	Saprovore (30%)	24.9	16.6	166	208
Coleoptera	Microbivore (50%)	74.9	49.9	291	416
Coleoptera	Predator (50%)	74.9	32.1	26.8	134
Acari, **total**		268	137	429	836
Gamasina	Predator (100%)	172	73.9	61.5	308
Uropodina	Microbivore (100%)	4.9	3.3	19.1	27.2
Prostigmata	Microbivore (75%)	5.1	3.4	19.8	28.3
Prostigmata	Predator (25%)	1.7	0.7	0.6	3.0
Astigmata	Microbivore (100%)	84.2	56.1	327	468
Cryptostigmata	Microbivore (100%)	0.1	0.1	0.4	0.6
Pauropoda	Microbivore (100%)	21.6	14.4	84.0	120
Microbivores		772	515	3,001	4,287
Saprovores		24.9	16.6	166	207
Predators		249	107	88.8	444
Enchytraeidae, **total**		5,100	3,400	26,917	35,417
Enchytraeidae,	Microbivore (50%)	2,550	1,700	9,917	14,167
Enchytraeidae	Saprovore (50%)	2,550	1,700	17,000	21,250

Note: Calculated, using $C = P + F + R$, from the respiration obtained when daily respiration values are summed for the whole incubation.

In the last two samplings aphids (Pemphigidae) were present. Their presence coincided with an ingrowth of roots into the bags. The aphids have not been considered when calculating abundance, biomass and respiration of arthropods (Fig. 2) since they are root feeders and do not participate in straw decomposition.

Microarthropod numbers per bag were lower during the second year, but if expressed as individuals per g remaining straw the abundances were similar for both years.

Within Eupodidae, *Eupodes* sp., *Cocceupodes paradoxus*, and *Protereunetes* sp. were identified. Coleoptera consisted of staphylinid larvae and adults, *Clivina fossor* (Carabidae) larvae and Elateridae larvae. Diptera larvae were represented by the families Chironomidae, Cecidomyiidae, Dolichopodidae and Fungivoridae. Chironomidae dominated in the November 1980 sampling and Fungivoridae in the last two samplings.

The Enchytraeidae decreased markedly in abundance in autumn 1981, mainly in the smallest size class. This indicates that reproduction had ceased in late autumn. In April 1980 the number of enchytraeids increased, mainly through an increase in the smallest length class, suggesting reproduction during early spring.

From September 1981 onwards the relative abundances of arthropod groups were, in general, unchanged. However, in the last samplings, Isotomidae decreased relative to Onychiuridae (mostly *T. krausbaueri s.l.*). When biomass instead of abundance was considered, Isotomidae dominated throughout the experiment. Astigmata were numerically the most important among the mites, followed by Gamasina and Prostigmata. Uropodina were found in low numbers and only a few specimens of Cryptostigmata were present. Gamasina dominated the biomass, especially when the large *Amblygamasus stramenis* was common. The Astigmata were second in biomass, followed by Uropodina. Prostigmata had a low biomass during the whole incubation. The few Coleoptera and Diptera found made up a considerable part of the total arthropod biomass, and the Enchytraeidae had a biomass that was one order of magnitude higher than the arthropod biomass.

Faunal density was higher in the litter-bags than in the surrounding soil. Since the exact volume of the litter-bag is not known, it is not possible to make an exact comparison, but a concentration factor of about five, for microarthropods in September 1981 and September 1982, was estimated. For enchytraeids this factor was around 10 in September 1981 and around three in September 1982.

All arthropod taxa found in the litter-bags were also found in the surrounding soil (J. Lagerlöf & O. Andrén unpubl.). However, the relative abundances were different in straw and soil (0 to 20 cm depth; Table 1). To examine if the differences were mainly due to a lack of surface-dwelling species in the litter-bags, the fauna at a depth of 2 to 20 cm were compared with the litter-bag fauna. The results were similar to those obtained when the whole soil profile was considered. Thus, only the comparison between the whole profile and the litter-bags is reported. Among Collembola, *P. minima* clearly had higher relative abundance in the litter-bags than in the soil both in 1981 and in 1982. *F. fimetaria* had a higher percentage in 1981, but not in 1982. *T. krausbaueri s.l.*, on the other hand, had a higher percentage in the litter-bags in 1982, but not in 1981.

Among the mites, most gamasid species showed somewhat lower relative numbers in the litter-bags. The Uropodina species *Nenteria breviangulata* was found only in the bags, but was rare even there. Of all arthropods, the astigmatid species *S. talpa* showed the greatest affinity for barley straw. All prostigmatid mites were less dominant in litter-bags than in soil, or were recorded only in the soil. The relative abundances of Symphyla, Pauropoda and Diptera larvae were lower in straw than in soil. Enchytraeids in the smallest size class were relatively more abundant in the bags than in soil.

Monthly respiration per litter-bag for arthropod groups and size classes of enchytraeids is shown in Fig. 2. The accumulated respiration of different species and higher taxa during the incubation is shown in Table 1. The influence of temperature on respiration is obvious (*cf.* Fig. 1). Among Collembola, Isotomidae contributed most to total respiration, followed by Onychiuridae, Entomobryidae, Poduridae and Sminthuridae in decreasing order. Gamasina gave the greatest contribution among the mites, followed by Astigmata, Prostigmata and Uropodina. Respiration sums for Pauropoda, Protura and Diplura were intermediate between Astigmata and Prostigmata. Respiration by Coleoptera and Diptera was equal to that of Acari during 1981 but fell to about 50 % of the acarid respiration in 1982. Estimates of respiration, production, defecation and consumption for higher taxa and trophic groups are shown in Table 3. The total respiration by Enchytraeidae during the experiment was calculated to be 0.8 % and the arthropod respiration 0.2 % of the total carbon loss from the straw material.

4. Discussion

The litter-bag technique is well suited for investigations in arable land, since ploughing creates similar concentrations of straw and stubble.

In the present investigation, with all litter-bags incubated at 10 to 15 cm depth, seasonality had no major influence upon species composition, except for a decline for most species in the smaller size classes during autumn. This decline may be interpreted as the end of the breeding season. The position of the bags below ground stabilized moisture conditions during the incubation, with water content ranging from 50 to 65 % of the wet mass (Sohlenius & Boström 1984). Thus moisture never became a limiting factor, which can occur if bags are put on the surface. It is impossible to know whether nutritional or structural properties of the straw were most important in determining the species composition in the litter-bags. Larger animals, e.g., the gamasid predators, may benefit from the loosely-packed structure of straw as compared to the denser soil. Predators were important in the litter-bags since they accounted for a large part of the energy flow through the microarthropod community (Table 3) and it is possible that they keep their prey well below abundances where food, breeding sites, etc., become limiting.

According to the results, the arthropods may be divided into three groups in relation to their affinity to the straw. The first group consists of taxa that are strongly attracted *(P. minima, N. breviungulata* and *S. talpa)*. They are known to be associated with organic matter (Evans *et al.* 1979; Fjellberg 1980), and the two mite species are seldom found in mineral soil. Possibly Anoetidae can be included in this group.

The second group of arthropods shows higher abundance in straw than in soil but their relative abundance is not different from that in soil. Most Collembola and Gamasina belong to this group, which is part of the general soil and litter fauna not specialized for rapid colonization.

The third group of arthropods that may be distinguished has a lower relative abundance in straw than in soil. Prostigmata, Pauropoda, Protura and Diptera belong to this group. This group may have low competitive ability when food resources are ample but survive in mineral soil with less microbial food. Their small size (excepting Diptera) also makes it possible for them to occupy the small pores found in the mineral soil.

When frost periods were excluded, straw decomposition rate showed a typical pattern, with an initial rapid mass loss rate until July 1981 and a somewhat lower rate towards the end of 1981. In 1982 the decrease in rate continued (Wessén & Berg 1985).

During the first part of 1981 only a few microarthropod species colonized the litter-bags. The fauna was dominated by bacterial-feeding nematodes which reached high densities, and the total nematode density per bag was highest in June 1981 (Sohlenius & Boström 1984). The bacterial production was also high during this period (O. Andrén *et al.* unpubl.) This is in accordance with the early colonization by Anoetidae (Table 1), which feed on the slimy surfaces of wet organic material, where bacteria are probably a major constituent (Krantz 1975). *Alliphis siculus*, a nematode predator (Karg 1983), also had an early maximum. The later decrease in abundance of these species may be correlated with the decrease in bacterial production and nematode density (Sohlenius & Boström 1984). The occurrence of chironomid larvae in the first sampling coincided with high abundances in the soil (Carter *et al.* 1985). Thus their occurrence in the straw does not necessarily indicate an affinity for a certain stage of straw decomposition. In contrast, the enchytraeid maximum in June and July 1981 may be substrate-dependent, since enchytraeids are believed to be associated with organic matter and to consume both bacteria and decomposing organic matter (Persson *et al.* 1980). The majority of microarthropods, being mainly fungivorous, increased in abundance somewhat later, when fungal biomass started to increase (Wessén & Berg 1985). After September 1981 the microarthropod abundance was fairly constant. The species composition was also remarkably stable after September 1981. However, the observation that *V. exigua, I. notabilis* and *I. minor* increased towards the end of the study may indicate a preference by these species for a more decomposed material. *V. exigua* also increased in the

surrounding soil, but it should be remembered in all interpretations that there was organic matter of the same age in the soil, ploughed under at the same time as the incubation of litter-bags. Furthermore, in spring 1982 stubble and roots were mixed into the soil, representing a new input of organic matter (see sect. 2).

The succession of faunal groups in the present experiment appears to be mainly a result of substrate changes and related changes in microbial production. The constant microarthropod species composition after peak density may be a consequence of the slow change in substrate properties at that time. Arable land harbours an impoverished fauna due to, e.g., the lack of a litter layer. This creates a lower immigration pressure than in other environments, which may partly account for the constant species composition. In addition, the placement of the litter-bags at a depth of 10 to 15 cm certainly also affected the immigration pressure.

Succession patterns in decomposing plant residues in arable soil are reported in a number of papers. NAGLITSCH (1966) distinguished between three phases in decomposition of lucerne and rye straw in soil, characterized by different microarthropod and nematode communities. First there was a colonization phase, when Diptera were found, especially in substrates rich in nitrogen. Then there was a decomposition phase dominated by nematodes, nematode-consuming Gamasina and some other mite families, e.g., Anoetidae. This phase changed after a few weeks into the humification stage, which according to the author started when hypopus nymphs of Anoetidae began to occur. In the humification stage Collembola, Gamasina that fed on these, Uropodina and Cryptostigmata increased gradually.

EITMINAVIČIŪTĖ *et al.* (1976) found a similar pattern when they studied lupin and straw decomposition in arable soil. A microbial phase during the first 20 days was followed by a general microarthropod phase from 20 to 140 days, when bacteria numbers declined and the amount of cellulose decomposing fungi increased. The decomposition rate was still high, but decreased towards the end of the period. During this period microarthropod biomass rose and a continuous succession was observed. In the late part of the investigation, 140 to 650 days, Cryptostigmata and tarsonemid mites dominated and decomposition rate was low. An increase in Actinomycetes was observed during this period.

TÖRNE (1964) studied collembolan activity during wheat straw decomposition in different soils during different seasons. This author concluded that microbial successions and successive substrate changes had greater impact on the collembolan community than season or humidity, i.e., true succession occurred.

In an earlier investigation at kjettslinge (ANDRÉN & LAGERLÖF 1983) early colonizers such as astigmatid and uropodid mites were common after two and four months. Animal groups typical for the surrounding soil, e.g., Prostigmata and Pauropoda were more abundant after 12 months. This succession may have been part of an overall succession in the soil at that time, due to the installation of tile-drainage and the rapid decrease in soil mineral nitrogen when barley was grown without nitrogen fertilizer (BERGSTRÖM 1982). In the present investigation no such clear successional changes were found, but by this time the field had reached more stable conditions. Another important difference was that in the first experiment the bags were incubated in June instead of November. Since there was low activity during winter, some of the difference in results may be attributed to this. However, the annual decomposition rate, microarthropod species number and maximum abundance were similar in both studies.

Patterns of microarthropod succession similar to those found in arable land are also found in other ecosystems. However, the succession due to substrate changes was often found to be less important than, or inseparable from seasonal fluctuations (WIEGERT 1974; VOSSBRINCK *et al.* 1979). Humidity and structural properties of the substrate were found to be more important than nutritional properties by GILL (1969), ANDERSON (1975), MIGNOLET & LEBRUN (6975) and STEVENSON & DINDAL (1980). GILL (1969) suggested that microarthropods are kept at such low abundances by predators, that food never becomes limiting or, alternatively, that nutritional factors not related to litter decomposition are limiting.

The role of enchytraeids in organic matter decomposition has not been studied as much as the role of other soil animals (KASPRZAK 1982). ANDERSON (1975) found an increase towards

the end of the incubation period (12 to 19 months) and, for the whole period, a positive correlation with substrate moisture. Most authors have found rather high abundances during early decomposition (ALEJNIKOVA *et al.* 1975; HUHTA *et al.* 1979) which is in agreement with the present investigation.

The observation in the present study that diversity (H') and equitability (E) reached maxima before abundance reached its maximum and, thereafter, remained constant is in agreement with the results reported by ANDERSON (1975) and HÅGVAR & KJÖNDAHL (1981). This is a consequence of the immigration of many species in low numbers and a later reproduction of only a few of these species. Among the most common species individual biomass decreased with time, which indicates that these reproduced within the bags. In the long run it may be expected that diversity decreases as the substrate disappears, but this stage was not reached in the present study.

The contribution from nematode respiration to carbon loss from the litter-bags during the whole incubation was around 0.2% (SOHLENIUS & BOSTRÖM 1984). In spite of the diverse microarthropod community, the microarthropods contributed only 0.2% to total carbon loss. The enchytraeids contributed 0.8%. The mesofaunal component in carbon mineralization may seem to be insignificant, but during this period the rate of carbon loss from the bags steadily decreased, whereas microarthropod and enchytraeid abundance was fairly constant. Thus the relative contribution of these groups increased with time, a subject that will be further analyzed by O. ANDRÉN *et al.* (unpubl.).

Finally, another important aspect is that the microarthropod community in the litter-bags consisted mainly of microbivores and predators, which consume nutrient-rich food and thus release nutrients (PERSSON 1983). This release of nutrients may be of importance for plant growth, especially at times when the availability of nutrients in the soil is low.

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J. LAGERLÖF was responsible for the enumeration and identification of soil fauna and had the main responsibility for the synthesis. O. ANDRÉN was responsible for the computerized calculations. Both authors are equally responsible for the design and realization of the project, as well as for the conclusions.

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Synopsis: *Original scientific paper*

LAGERLÖF, J., and O. ANDRÉN, 1985. Succession and activity of microarthropods and enchytraeids during barley straw decomposition. Pedobiologia **28**, 343—357.

The abundance of microarthropods and enchytraeids in litter-bags with decomposing barley straw was followed for two years. The bags were incubated in late autumn 10 to 15 cm under a barley monoculture. After two years the barley straw had lost 63 % of its initial mass.

Enchytraeidae colonized faster than most microarthropods and had the highest biomass during the first summer. Arthropod species composition changed between the early phase (first autumn, spring and summer) and later phases of decomposition, and was possibly related to substrate changes. After the early phase arthropod species composition and diversity were similar between samplings. Collembola and astigmatid mites dominated in abundance, while gamasid mites dominated in biomass.

Collembola had higher body masses in early samplings than in later samplings, indicating that adults colonized the litter-bags and then reproduced. The numbers of arthropods and enchytraeids per unit volume were higher in the straw than in the surrounding soil.

Contributions to total carbon loss were small, 0.8 % for enchytraeids and 0.2 % for microarthropods.

Key words: Soil fauna, Acari, Collembola, Diptera, Pauropoda, abundance, biomass, diversity, respiration, species composition, succession, arable soil